The impacts of forestry on polyporous fungi in boreal forests

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Academic dissertation

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List of articles

This thesis is a summary of the following papers, which are referred to by their Roman numerals.

I Penttilä, R. and Kotiranta, H. 1996: Short-term effects of prescribed burning on wood-rotting fungi. – Silva Fennica 30 (4):399-419.

II Penttilä, R., Siitonen, J. and Kuusinen, M. 2004. Polypore diversity in managed and old-growth boreal *Picea abies* forests in southern Finland. – Biological Conservation 117: 271-283.

III Siitonen, J., Penttilä, R. and Kotiranta, H. 2001. Coarse woody debris, polyporous fungi and saproxylic insects in an old-growth spruce forest in Vodlozero National Park, Russian Karelia. – Ecological Bulletins 49: 231-242.

IV Penttilä, R., Lindgren, M., Miettinen, O., Rita, H. and Hanski, I. 2004. Consequences of forest fragmentation for polyporous fungi at two spatial scales. – Manuscript.

Contributions

The following table indicates the major contributions of authors to the original articles or manuscripts.

	I	II	III	IV
Idea of the study	RP, HK	RP, JS, MK	RP, JS, HK	RP, IH
Material collection and identification	RP, HK	RP	RP, JS, HK	RP, ML, OM
Ideas and processing of analyses	RP	RP, JS, MK	RP, JS	RP, IH, HR
Manuscript preparation	RP, HK	RP, JS	RP, JS	RP, IH, HR

HK = Heikki Kotiranta, HR = Hannu Rita, IH = Ilkka Hanski, JS = Juha Siitonen, ML = Mariko Lindgren, MK = Mikko Kuusinen, OM = Otto Miettinen.

In addition, the identification of the most difficult polypore specimens in the material of all articles was confirmed by Tuomo Niemelä. Other contributors are acknowledged in the relevant articles or manuscripts.

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INTRODUCTION

Characteristic features of natural forests that are important for biodiversity in boreal Fennoscandia include forest fires, gap dynamics, large numbers of old, dead and deciduous trees, and long continuity of these features (Esseen et al. 1997). Furthermore, natural forest landscapes are characterized by large variation in the quality, size, severity, and repeatability of the various kinds of disturbances (Kuuluvainen 2002). Forest fire was a key disturbance factor for the regeneration of boreal coniferous forests before the era of modern forestry (Zackrisson 1977, Zackrisson & Östlund 1991, Esseen et al. 1997). In dry, pine-dominated forests the influence of fire has been especially important, and pine forests have burned more often than spruce forests in Fennoscandia (Zackrisson 1977, Engelmark 1984, Lehtonen et al. 1996, Ohlson and Tryterud 1999, Pitkänen et al. 2003, Wallenius 2004). Spruce-dominated forests are characterized by small-scale gap disturbance, gap regeneration, and high level of continuity of the characteristic ecological features (Kuuluvainen 1994), and spruce forests used to burn at intervals of hundreds or even thousands of years (Ohlson and Tryterud 1999, Wallenius 2002, Pitkänen et al. 2003, Wallenius 2004). However, starting some few hundred years ago and lasting until the effective fire suppression started at the end of the 19th century (e.g. Niklasson and Granström 2000), frequency of forest fires in Fennoscandia increased considerably both in spruce and pine forests due to human influence (Niklasson and Granström 2000, Pitkänen et al. 2002, 2003). Since the beginning of effective fire suppression, several attributes of forests that are associated with fires, such as high abundance of living and dead deciduous trees, have strongly diminished in Fennoscandian forests (Esseen et al. 1997). Perhaps the most important attribute of natural boreal forests for biodiversity is however great abundance of dead wood, which characterizes practically all forest types and successional stages in boreal forests (e.g. Esseen et al. 1997, Siitonen 2001).

The structure and dynamics of forests have been fundamentally transformed in Fennoscandia especially in the 20th century in the course of developing and intensifying industrial forestry (Esseen et al. 1997, Östlund et al. 1997). Although forests were rather heavily utilized in Finland for tar extraction and slash-and-burn cultivation, and there was extensive selective logging before the 20th century, the most significant changes in the structure of forests have occurred following the implementation of large-scale forestry with clearcuts since the Second World War (Kouki et al. 2001, Rouvinen et al. 2002). To take an example, Gu et al. (2002) found that roughly 75% of the original old-growth

spruce forests were lost in Kuhmo in eastern Central Finland from 1945 to 1995. The dominant changes in Fennoscandian forests have been severe fragmentation of previously extensive and continuous forest landscapes (but see Löfman and Kouki 2001), decrease in the amount of old-growth forest, development of even-aged stand structure, reduction in the abundance of deciduous trees and in numbers and volume of dead trees, and changes in disturbance dynamics due to elimination of forest fires (Berg et al. 1994, Esseen et al. 1997, Kouki et al. 2001, Siitonen 2001). The bulk of these changes can be attributed to differences in disturbance dynamics between managed and natural forests (Kuuluvainen 2002). While in managed forests the disturbed (harvested) areas and harvest rotation are rather regular, natural forests show much variation in the quality, size, severity and repeatability of disturbances (Kuuluvainen 2002).

The low amount and diversity of dead wood in managed forests in comparison with natural forests has adversely affected more species than probably any other recent change in Fennoscandian forests (Esseen et al. 1997). In modern managed forest landscapes, the remaining old-growth forest stands are often the only places where larger quantities and particular qualities of dead wood are present (Siitonen 2001). Since the area of old-growth has decreased dramatically during the last decades (Virkkala and Toivonen 1999, Kouki et al. 2001, Gu et al. 2002), a very large number of saproxylic species dependent on dead wood has become classified as threatened in Fennoscandia (Berg et al. 1994, Esseen et al. 1997, Gärdenfors 2000, Rassi et al. 2001). One of the most vulnerable groups is polypores, in which 37% of the species in Finland and 44% of the species in Sweden have been classified as threatened or near-threatened (Gärdenfors 2000, Rassi et al. 2001). For threatened polypore species the most detrimental factors in managed Fennoscandian forest landscapes are the scarcity of large dead trees (especially logs) and the small area of old-growth forests (Bader et al. 1995, Kruys et al. 1999, Sippola et al. 2001, 2004, Sverdrup-Thygeson and Lindenmayer 2003, Stokland and Kauserud 2004, this thesis).

Before the 1990's very few ecological studies on polypores were conducted, but the subsequent rise of biodiversity issues in forestry stimulated ecological studies on species dependent on dead wood in the 1990's. These recent studies on wood-decomposing fungi have mainly investigated how different qualities and quantities of dead wood affect species diversity, and the differences in species richness and abundance between managed and old-growth forests (Bader et al. 1995, Renvall 1995, Høiland and Bendiksen 1997, Ohlson et al. 1997, Lindblad 1998, Jonsson and Jonsell 1999, Kruys et

al., 1999, Kruys and Jonsson, 1999, Sippola and Renvall 1999, Sippola et al. 2001, Stokland 2001, Groven et al. 2002, Heilmann-Clausen and Christensen 2003, Nordén et al. 2004, Penttilä et al. 2004, Sippola et al. 2004, Stokland and Kauserud 2004). Only few studies have explored how fragmentation of old-growth forests (and stands with abundant dead wood) affects the occurrence of polyporous fungi (Komonen et al. 2000, Berglund and Jonsson 2001, Edman and Jonsson 2001, Lindgren 2001, Siitonen et al. 2001, Sverdrup-Thygeson and Lindenmayer 2003, Edman et al. 2004c, Rolstad et al. 2004; see also Högberg and Stenlid 1999, Edman et al. 2004 a, b). So far, there are no comprehensive studies on the effects of forest fire on species diversity of wood-decomposing fungi. Better knowledge of these subjects is urgently needed for conservation and forest management.

Aims of the study

The specific aims of this thesis are**:**

1) To investigate the short-term and long-term effects of forest fire on fungal communities and on individual species living on dead wood (I and Summary).
2) To compare species richness and the occurrence of threatened species between mature managed, “overmature” managed and old-growth forest stands and to analyse the relationships between stand characteristics and polypore communities (II).
3) To compare polypore communities between landscapes that differ with respect to the history of forestry and the amount of old-growth forests, to analyse the consequences of spatio-temporal isolation of old-growth stands for the occurrence and abundance of polyporous fungi within landscapes in which the fragmentation has occurred rather recently, and to analyse which species are especially sensitive to fragmentation of old-growth forest (III and IV).

This thesis also aims to contribute to a better understanding of the following general questions that are mostly connected to the conservation and management of forest landscapes. Is prescribed burning of forest an effective way to increase the amount of habitat for ecologically specialized and threatened polyporous fungi? Where should new conservation areas be located and where should forest restoration operations be made so that the benefit for rare and threatened species would be maximized? How much and

what kind of dead wood in forest stands is needed to ensure the survival of threatened species? What is the role of old-growth forests in the conservation of threatened species, and when does the amount of suitable habitat for the old-growth forest species become so low that the survival of these species is at risk?

MATERIAL AND METHODS

Study areas

The study areas are located in Häme, south-western Finland (I, II, IV), in Kainuu, east-central Finland (III, IV), in the Patvinsuo National park, east-central Finland (III), and in the Vodlozero National Park, Russian Karelia (III) (Fig. 1).

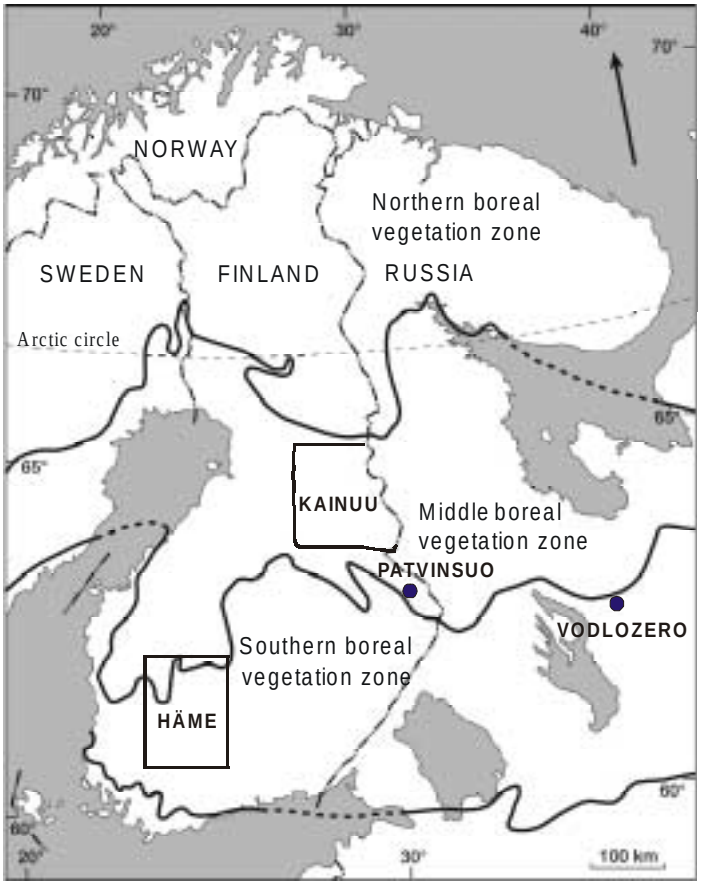

Fig. 1. Location of study areas in Finland and Russian Karelia. Vegetation zones are delineated according to Ahti et al. (1968) in Russia and Kalela (1961) in Finland.

All study sites belong to southern or middle boreal forest vegetation zones (according to Kalela 1961 and Eurola 1999). All studies included in this thesis were conducted in spruce-dominated forests with pine (*Pinus sylvestris*), birches (*Betula* spp.), aspen (*Populus tremula*) and goat willow (*Salix caprea*) as the most common other tree species. The study areas were mostly natural and semi-natural old-growth forests, but mature managed forests were studied in II and a burned forest area in I.

The study areas constitute a gradient in the impact of forestry and amount of old-growth forest in the landscape. In Häme in south-western Finland, the history of intensive forestry is longest, which is reflected in the very low amount of natural and semi-natural old-growth forests (0.3% of forest area; Virkkala et al. 2000) and low average amount of dead wood (~ 3 m^3/ha in all forested land area; Korhonen et al 2000 a,b). In Kainuu and in northern Karelia, where the Patvinsuo National Park is located, intensive forestry is more recent than in Häme, the proportion of natural and semi-natural old-growth forests is higher (2.9%; Virkkala et al. 2000) and the average amount of dead wood is twice as high (6.2 m^3/ha; Tomppo et al. 2003) as in Häme. The Vodlozero National Park in Russian Karelia represents a large area (5000 km^2) of natural taiga forest with abundant (over 40% of the area of the Park) old-growth forest and virtually no signs of forestry.

Sampling and classification of data

Fungi

The main study object of the present investigation was polyporous fungi. Paper I also includes all corticiaceous fungi (Corticiaceae), and IV includes two corticiaceous fungi (*Cystostereum murraii* and *Phlebia centrifuga*) and one hydnoid fungus (*Gloiodon strigosus*), which have been widely used as indicators of old-growth forest in Fennoscandia (e.g. Karström 1992, Kotiranta and Niemelä 1996, Bredesen et al. 1997). Field work was conducted in September and October, when both the annual and perennial fruiting bodies of polypores and corticiaceous fungi occur at their maximum numbers. In all papers both species richness and abundance of fungi were studied. The abundance of each species was recorded as the number of tree trunks on which the species was found, and hence one or more living or recently dead fruiting bodies on one trunk represents one individual. In reality, different fruiting bodies growing on the same trunk do not always belong to same fungal individual (Rayner & Todd 1977, 1979), but in ecological studies

covering large areas it would be impractical to try to critically identify different biological individuals.

While a thorough investigation of all dead wood in a sample plot evidently reveals all visible species and individuals of fungi most effectively, this method is generally too laborious and ineffective in studies focused on rare, threatened and indicator species in large areas. The occurrence of rare, threatened and indicator species was of special interest in II, III and IV, and hence potential host trees for such species, including all large and much-decayed logs, were carefully inspected, while recently fallen and small logs were investigated less thoroughly. In the managed forests studied in II also recently fallen and small logs and even cut stumps were carefully inspected.

For the analyses in II, III and IV polypores were classified into several species groups based on their general occurrence in managed and natural forests (as reported in previous studies). Both species number and pooled abundance of individual species in these groups were analysed. All species, threatened species and near-threatened species were the species groups that were analysed in the greatest detail. In I threatened and near-threatened species are classified according to Rassi et al. (1992), in III according to Kotiranta and Niemelä (1996) and in II and IV according to Rassi et al. (2001).

Environmental variables

The environmental variables were mainly related to the characteristics of the quality and quantity of dead wood. In I dead wood variables such as tree species, form (quality), size (diameter at breast height), decay stage, amount of epiphytes, signs and degree of fire and the amount of bark were inspected on individual trees at the same time when the inventory of the fungi was made. In II, III and IV dead wood variables were measured at stand level and polypore inventories were done separately. Besides the dead wood variables, forest type (III), living trees (II, III and IV), numbers of cut stumps (II, III and IV), mean age of dominant trees (II and IV) and the area of swampy forest (IV) were measured. For the analyses, several derived variables describing the quality and quantity of dead wood were calculated. Depending on the type of dead wood, the quantity was calculated either by using volume (m^3/ha) or the number of trunks, and the quality was expressed by the diversity of dead wood types and by the number of soft logs (decay classes IV and V; continuity of dead wood in a sample plot).

Data analyses

Fungal communities before and after fire were compared in terms of species abundance distributions, Shannon-Wiener diversity index and percentage similarity index (I). Differences in species number in different dead wood categories before and after the fire were tested with a non-parametric sign test (I). In II Kruskal-Wallis non-parametric analysis of variance was used to test differences in the numbers of species and individuals in different species groups among mature, overmature and old-growth stands. Throughout the thesis, I used mainly non-parametric instead of parametric tests, because in most cases the dependent variables (number or abundance of species) were not normally distributed.

Relationships between the stand variables and the species richness of polypores in different species groups in II were first screened with Spearman's rank corre lations. Then the relationships between species numbers and different stand variables were analysed either with linear regression (number of all species) or with generalized linear model (GLIM) with a Poisson error distribution and a logistic link function (number of threatened species). Variation in species composition among the sample plots was investigated with non-metric multidimensional scaling (NMDS; II). In IV a metapopulation model was used to derive a measure of isolation of a forest fragment that is influenced by the history of fragmentation during a 50 year period. To compare species richness and pooled abundance in different groups of polypores between the Kuhmo and Häme study areas and among old-growth forest fragments within the Kuhmo study area I used a generalized linear model with a Poisson error distribution and a logistic link function (IV).

RESULTS AND DISCUSSION

Fire and wood-decomposing fungi

Forest fire is a large-scale disturbance factor, which typically has a destructive direct, short-term effect on fungal communities (Parmeter 1977, Pugh and Boddy 1988, Watling 1988, Wicklow 1988). Severe fire destroys fungal mycelia and decreases the inoculum potential of many fungi by reducing the amount and quality of dead woody material and by creating extreme environmental conditions (Parmeter 1977, Pugh and Boddy 1988). In severely burned forests, maximum temperatures are high, insolation is high and humidity

is low (Parmeter 1977), and in general the environmental conditions become more extreme and variable than in old, closed forests. In burned forests environmental heterogeneity tends to decrease, which in turn is likely to lead to lower species richness and diversity in fungal communities (Zak 1991). Severe disturbance such as forest fire is expected to increase dominance of a limited number of species in the community (Odum 1985).

Consistent with the these general expectations, species number and species (Shannon-Wiener) diversity indeed decreased, and the evenness of the Shannon-Wiener diversity increased, in the fungal communities in the severely burned forest area in Evo (I). Similar destructive short-term effects of fire on the communities of wood-decomposing polypores were found in a study of fungal succession following forest fire in the Patvinsuo National Park, eastern Finland (Penttilä unpublished, Fig. 2). In this study two small (1 ha) forested islands in the midst of the open mire were burned for research purposes in early summer 1989. One site was a mixed, pine-dominated old-growth stand while the other one was a pine-dominated managed stand. Polypores were inventoried in both islands in 1988, one year before the fire, and in 1989, 1990, 1991, 1995 and 2002 following the fire. Some results of this study will be described below.

While fire is destructive for resident fungal communities, fire also provides a large input of organic matter and new resources for decomposers in the ecosystem, and in doing so fire acts as enrichment disturbance (Pugh & Boddy 1988). Indeed, the amount of dead wood in natural boreal forests is usually at its highest in early successional stages right after large-scale disturbances, such as forest fires and storm disturbance (Spies et al. 1988, Uotila et al. 2001, Siitonen 2001). In the burned forest islands in the Patvinsuo National Park, and especially in the old-growth forest island, fire killed most of the living trees and created a large input of new resources for fungi. The positive effect of the resource input on species number and diversity of wood-decomposing fungi became evident after some years. In Patvinsuo, where the amount of dead wood after the fire was at least two to three times higher than before the fire, it took six years for the species number to recover to the same level as before the fire (Fig. 2). Thirteen years after the fire the positive effect of dead wood accumulation on polypore diversity was evident. While the total number of polypore species in both forest islands was 53 one year before the fire, altogether 75 polypore species were found 13 years after the fire (Fig. 2). Even more striking was the increase in the numbers of red-listed species (threatened and near-threatened species; Rassi et al. 2001), from 12 species before the fire to 23 species 13

years after the fire (Fig. 2). The time delay in the accumulation of species after the fire can be easily explained by the fact that it takes several years or even decades for the fire-killed trees to reach the more advanced stages of decay, in which both the species number and species diversity is higher than in fresh and slightly-decayed trees (Bader et al. 1995, Renvall 1995, Høiland and Bendiksen 1997). Threatened and near-threatened polypore species in particular are dependent on logs in the more advanced stages of decay (Bader et al. 1995, Kruys et al. 1999).

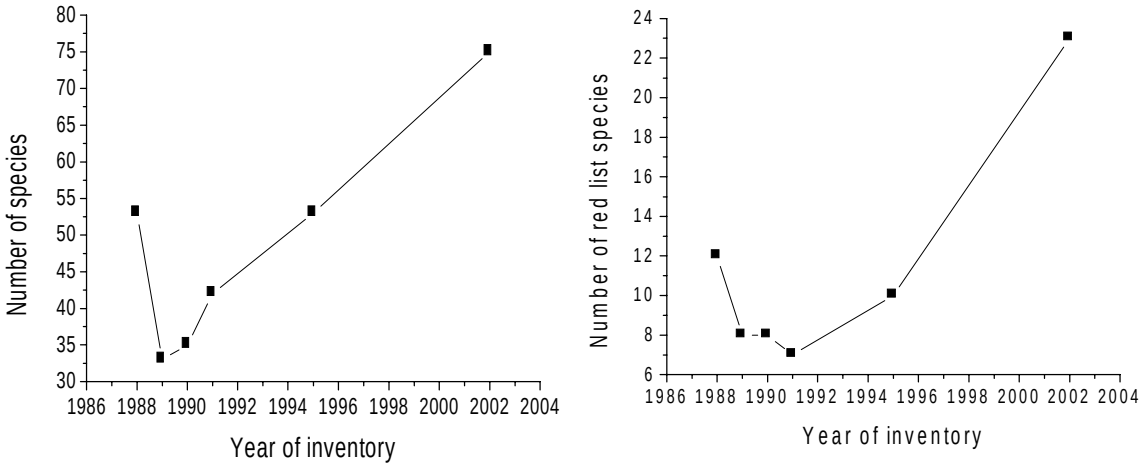

Fig. 2. The response of polypore species to forest fire and the long-term change in species number in two burned, pine-dominated forest islands in the Patvinsuo National Park. Red-listed species are according to Rassi et al. (2001) and they include both threatened and near-threatened species.

The elimination of forest fires has evidently been most detrimental to species which are dependent of (anthracobiont species) or which favour (anthracophilous species) fires (e.g. Esseen et al. 1997). Fire-dependent fungi belong mainly to the class Ascomycetes, but a few agarics are also included (Moser 1949, Ebert 1958, Petersen 1970, Wicklow 1975). Among the wood-decomposing fungi there are hardly any fire-dependent species in Fennoscandia (Eriksson 1958), but several species appear to benefit of fire (Eriksson 1958, Renvall 1995). In general, disturbances are expected to favour ruderal species at the cost of competitive species (Odum 1985, Rayner & Boddy 1988).

In addition to ruderal species, species surviving the extreme conditions created by severe fires (stress-tolerant species; Cooke and Rayner 1984) are expected to flourish in burned areas. In support of these expectations, the species that were favoured by fire (I) were mostly ruderal corticiaceous species (e.g. several species of *Athelia, Botryobasidium obtusisporum, Chondrostereum purpureum, Cylindrobasidium laeve, Phanerochaete raduloides*), which appear to be able to utilize effectively the new, competition-free substrates generated by fire. However, new information on *Athelia* species (Stokland pers. comm.) suggests that these species are probably not ruderal but mycorrhizal species, which start to produce fruiting bodies after the fire as a mechanism to escape the moribund tree association, in the same manner as the post-fire ascomycete *Geopyxis carbonaria* (Vrålstad et al. 1998). The results in I and in the study conducted in the Patvinsuo NP demonstrate that fire favoured those polypore species that thrive in dry, open areas such as pine-dominated forests and clear-cut areas (e.g. *Antrodia sinuosa, Antrodia xantha, Dichomitus squalens, Gloeophyllum sepiarium* and *protractum, Postia placenta, Pycnoporus cinnabarinus, Trametes hirsuta*). Some of these species are rather common also in areas that have not been affected by fire, but some species are presently rare (e.g. *D. squalens, G. protractum, P. placenta, Physisporinus rivulosus*), and lack of forest fires most probably has contributed to their rarity.

Those species that suffer of forest fires (anthracophobe species) are expected to be among the most competitive species (Odum 1985, Pugh and Boddy 1988, Rayner and Boddy 1988), which often prefer logs in the more advanced stages of decay (Pugh 1980, Holmer et al. 1997). Conditions in old-growth forests favour competitive fungal species (Grime 1979, Pugh 1980), and species that do well under these conditions may do poorly under stressful conditions and following large-scale disturbances (Cooke & Rayner 1984). The results in I are consistent with these conjectures. Species occurring in logs of advanced decay stage suffered more of fire than species occurring in less decayed logs. All threatened polypores as well as other polypore species that have been classified as old-growth species in Finland (Kotiranta and Niemelä 1996) also declined strongly after the fire; these species typically prefer more advanced decay stages and they did not produce fruiting bodies one year after the fire. These results could be explained by the tendency of decayed logs to burn more effectively than non-decayed logs (Parmeter 1977). Another explanation might be that fire-induced changes in the moisture content of logs are more critical for species growing in late stages of decomposition, since these species are adapted to live in moister conditions than species using fresh logs. Water

content and water availability for fungi in fallen logs increase considerably with increasing decay (Maser & Trappe 1984, Dix 1985, Sollins et al. 1987, Renvall 1995). Furthermore, since the species that have been classified as old-growth species in Finland (Kotiranta and Niemelä 1996) decreased the most, the greatly altered environmental conditions in general in the forest stand, and not only the conditions in a particular log, may be most harmful for these species.

While the results on the short-term effects of fire in I indicate that the species number and abundances of especially old-growth species are reduced by fires, the long-term results from the Patvinsuo study area are to some extent conflicting. Of the numerous threatened and near-threatened polypore species that were found 13 years after the fire (Fig. 2), several have been classified as old-growth or old forest species, supposed to thrive almost exclusively in spruce-dominated old-growth forests (Kotiranta and Niemelä 1996). Some of these species, including *Crustoderma dryinum, Fomitopsis rosea, Perenniporia subacida, Phellinus ferrugineofuscus, Postia placenta*, were actually rather abundant, which implies that some of the supposedly old-growth species do not necessarily require the moist and stable old-growth conditions to survive and produce fruiting bodies. In fact, for some of these red-listed species abundant and continuous availability of dead wood per se might be more important than the moist and stable conditions of old-growth forests. It is notable, however, that in Patvinsuo the majority of the red-listed species that were found in the burned forest islands are rather abundant also in the nearby old-growth forests (III) and hence the sources of colonization may have been large. It remains unclear what is the optimal habitat for these species, but in any case the results demonstrate that they are able to colonise and survive also in burned (and open) areas. Similar observations have been made also for other wood-decomposing fungi (Sippola and Renvall 1999, Martikainen et al. 2000), and several studies on beetles have shown that dead wood in open and sunny areas can host a large number of red-listed species (Kaila et al. 1997, Jonsell et al. 1998, Martikainen 2001, Sverdrup-Thygeson and Ims 2002), of which several have been previously classified as species living exclusively in mature and old-growth forests (Rassi et al. 1992, Kouki et al. 2001).

Polyporous fungi in managed and old-growth forests

The polypore assemblages in natural or semi-natural old-growth forest stands were compared with assemblages in managed mature stands in II. The old-growth stands had

on average 80% more of polypore species than mature stands and 38% more of species than “overmature” managed stands (II). Previous comparisons of wood-decomposing fungal communities in old-growth and managed forests have revealed similar differences. Lindblad (1998) found 137% more species, Jonsson and Jonsell (1999) 62% more, and Sippola et al. (2001) 72% more species in old-growth than in mature or “overmature” managed stands. Since a part of the potential substrate in the old-growth stands was not carefully studied because of the very high amount of dead wood, a complete inventory would probably have yielded even more individuals (probably 10−30%) and also a few more polypore species per plot. Hence, the present study was slightly biased against high diversity in old-growth stands, which means that the results in II are conservative. Apart from wood-decomposing fungi, studies on other saproxylic species, including mycetophilids (Økland 1994), beetles (Siitonen 1994, Martikainen et al. 1999, 2000) and bryophytes (Gustafsson and Hallingbäck 1988, Andersson and Hytteborn 1991), have shown that species richness is clearly higher in old-growth than in managed forests.

The number of dead trees with DBH ≥ 10 cm per ha, diversity of dead wood, total volume of dead fallen logs, and total volume of dead wood had the highest correlations with the number of fungal species in the forest stands studied (Table 2 in II). However, these correlations must be interpreted with caution, because most of the variables are strongly intercorrelated. In regression models diversity of dead wood alone explained 85% of the variation in the number of all polypore species, and none of the other variables significantly increased the fit of the model (II). Number of dead trees and the volume of dead wood explained almost equally well the observed variation in species richness, but adding the diversity of dead wood and the volume of dead deciduous trees to these models slightly increased the fit of the model (II).

Both the volume of dead wood and the number of dead trees have been shown to be important variables in predicting species richness of several groups of species associated with dead wood habitats (Bader et al., 1995; Økland, 1996; Økland et al., 1996; Ohlson et al., 1997; Sippola and Renvall, 1999; Martikainen et al., 2000; Stokland, 2001, Sippola et al. 2004). The importance of dead wood diversity as calculated in II has also been investigated for saproxylic beetles by Martikainen et al. (2000) and Similä et al. (2003). The results of Similä et al. (2003) and those in II show that the diversity of host tree types (the number of different niches available; see e.g. Hutchinson 1959) is of great importance in explaining species richness of saproxylic beetles and polypores, respectively, at the stand level (see also Siitonen 2001).

Deciduous trees and species dependent on deciduous trees are an important element of biodiversity in Fennoscandian forests (e.g. Esseen et al. 1997, Kuusinen 1995, Kouki et al. 2004). In this study (II), the abundance of dead deciduous trees was an important factor in explaining species richness of polypores. In fact, the difference in species richness between mature and overmature stands in II was almost entirely due to species dependent on deciduous trees. In old-growth stands, large aspen (*Populus tremula*) logs, which were almost entirely absent in mature and overmature stands, hosted some additional species not found in other types of forest.

Sippola et al. (2004) found in a study of polyporous fungi in subxeric, mesic and herb-rich forests and spruce mires in northern Finland that 57% of the total species richness was found on deciduous trees. Large living or dead deciduous trees, especially the aspen, have been found to be key tree species for the diversity of several groups of species in old-growth boreal forests, including epixylic bryophytes, epiphytic lichens and saproxylic insects (Andersson and Hytteborn, 1992; Siitonen and Martikainen, 1994; Kuusinen, 1995; Esseen et al., 1997; Kuusinen and Siitonen, 1998, Kouki et al. 2004).

Species composition of polypores differed greatly especially between the different kinds of forest stands (Fig. 2 in II). Species thriving in managed forests are mainly species that are able to use cut stumps and logging residues. *Heterobasidion parviporum*, a serious pathogen of living spruce causing high economic losses in managed forests (Woodward et al., 1998), was found almost exclusively in cut stumps in managed stands. On the other hand, no threatened species were found in cut stumps or thin logging residues. Threatened species were almost entirely found in old-growth forests and in large-diameter logs of *Picea abies, Pinus sylvestris* and *Populus tremula* in more or less advanced stage of decay (II). These results are consistent with those of previous studies showing that most red-listed wood-living species do not utilize fine woody debris, and that large logs are especially important for threatened and rare wood-living species (Gustafsson and Hallingbäck, 1988, Bader et al., 1995, Jonsell et al., 1998, Kruys et al., 1999, Kruys and Jonsson, 1999, Sippola et al., 2001, Sippola et al. 2004).

In the statistical model, the number of cut stumps was the best explanatory variable for the species richness of threatened species (negative effect), followed by variables describing the number, volume and diversity of dead trees (Table 4 in II). The order in which the explanatory variables enter regression models is likely to be sensitive to the relatively small number of stands studied. Nevertheless, the number of cut stumps may reflect the long-term management history and continuity of dead wood better than

other variables describing the current status of dead wood (see also Siitonen et al., 2000). Significant negative effect of previous logging activities on species richness of all or threatened polypores has been previously demonstrated by Bader et al. (1995) and Sippola et al. (2001, 2004). Stokland (2001) and Stokland and Kauserud (2004) have shown that previous forest management history, as indicated by a specific coarse woody debris profile, has an important effect on the presence and abundance of threatened polypore species. On the other hand, Ohlson et al. (1997), Groven et al. (2002) and Rolstad et al. (2004) failed to find a positive correlation between dead wood continuity and richness and abundance of indicator and threatened wood-decomposing fungi at stand level. It may be that continuity of dead wood within the dispersal distance is more or at least equally important for threatened wood-decomposing fungi than stand-level continuity (see also Norden and Appelqvist 2001, Sverdrup-Thygeson and Lindenmayer 2002). The occurrence of threatened old-growth forest species in the burned forest stands in the Patvinsuo National Park (above) supports the view that continuity of the ecological conditions at the stand level is not of critical importance to many of the threatened polypore species, probably as long as isolation does not prevent colonization from outside the focal stand.

The threshold concept for long-term persistence of populations has been used in landscape ecology and conservation biology to describe the minimum amount of suitable habitat or resource necessary for a population of a particular species to persist in a landscape (extinction threshold: Lande, 1987; Hanski et al., 1996; Fahrig, 2002). Somewhat confusingly, the threshold concept has also been used to refer to the amount of suitable habitat in a landscape below which adverse effects of habitat loss and fragmentation on population density first become apparent (also called fragmentation threshold: Andrén, 1994; With and Crist, 1995; Jansson and Angelstam, 1999). The threshold concept can also be applied at smaller scales, for example at the stand level, to describe the minimum amount of resource that is required for a population to persist locally.

In II, threatened species were not found in stands in which the amount of dead wood was less than 20 m^3/ha. This figure thus appears to represent an approximate threshold value for the amount of dead wood below which the persistence or colonization of threatened polypore species becomes unlikely due to low density of potential host trees. Naturally, the actual threshold values are species-specific and likely to vary across different landscapes depending on e.g. forest type, matrix quality and the amount and

spatial configuration of suitable habitat in the surrounding landscape (Fahrig and Merriam, 1994; Andrén et al., 1997; Mönkkönen and Reunanen, 1999; With and King, 1999; Fahrig, 2001). For instance, in central-eastern and northern Finland, where both the amount of old-growth forests and the amount of dead wood in managed forests are higher than in the study region in Häme, the threshold value for the occurrence of threatened polypore species may be lower than 20 m^3/ha. On the other hand, in the southernmost Finland, where the amount of old-growth forests is even smaller than in Häme, a higher threshold level than 20 m^3/ha may apply. Considering the generality of the value 20 m^3/ha, it is noteworthy that Punttila (2000) and Siitonen and Punttila (2003) found in a study made in the same area as II approximately the same threshold value (20 m^3/ha) in the amount of coarse woody debris at the stand level for the occurrence of two saproxylic beetles (*Olisthaerus substriatus* and *Harminius undulatus*). Korhonen (2004) studying mature pine-dominated forests in Pohjois-Häme, Kainuu and Vienansalo Wilderness in Russian Karelia found practically no threatened or near-threatened saproxylic beetle species in stands in which the amount of dead wood was less than 35 m^3/ha. Angelstam et al. (2003) and Bütler et al. (2004) suggest that the persistence of the three-toed and the white-backed woodpeckers in Poland, Sweden and Switzerland require that snag and dead wood volumes exceed 10–20 m^3/ha over at least 100 ha of forest. In summary, although the exact figure will evidently vary from one taxon to another, and from one forest region to another, there is some generality in the threshold value of around 20 m^3 of dead wood per ha.

Extended rotation time leading to “overmature” forest stands has been advocated as a method to preserve species associated with late-successional forest stages (Curtis, 1997; Seymour and Hunter, 1999). Although such overmature stands have a higher average number of polypore species than the mature stands, these two categories of managed forests did not differ from each other with respect to the numbers of threatened and near-threatened species (Table 3 in II). The results in II suggest that stand structure, in particular the amount and quality of dead wood, is by far a more important factor for polypore communities than stand age per se. However, prolonging the rotation time by 30−50 years may benefit those polypore species that utilise deciduous host trees, which become senescent and start to die earlier than coniferous trees in managed stands.

Fragmentation of old-growth forests and polyporous fungi

The extensive loss and fragmentation of old-growth forests particularly in southern Fennoscandia can be expected to affect especially severely dead-wood dependent saproxylic species, including polypores, since old-growth forests are the only places in the managed Scandinavian forest landscapes where large quantities and diverse qualities of dead wood still exist (Siitonen 2001). The threatened species of polypores in particular should show strong negative responses to the loss and isolation of old-growth forests, since these species are very seldom found in managed forests (Kruys and Jonsson 1999, II). Habitat destruction for any given species may include pure habitat loss and increasing fragmentation of the remaining habitat, but also deterioration of habitat quality (Saunders et al. 1991, Hanski 1999). Habitat fragmentation, which can be defined as decreasing fragment size and increasing degree of isolation among the fragments (Andrén 1997), typically occurs together with habitat loss (Forman 1995). In the early stages of habitat fragmentation, when there is still a considerable amount of suitable habitat remaining in the landscape, population sizes of individual species decrease in proportion to the change in the amount of suitable habitat (Andrén 1994, 1996). Considering the threshold amount of habitat below which fragmentation effects become apparent, Andrén (1994) concluded that when less than 10-20% of the original habitat is left at the landscape scale, the abundances of forest birds and mammals decline faster than in proportion to the amount of habitat with further decline in the amount of habitat.

Even though threshold levels and responses to habitat fragmentation are species-specific (e.g. Andrén et al. 1997, Mönkkönen and Reunanen 1999), a similar result was obtained in III: the abundances of threatened polypore species were about three times lower in a landscape (Kainuu, eastern Finland) in which the amount of suitable habitat (old-growth forest) was under 10% at the landscape level in comparison with another forest landscape (Vodlozero National Park in Russian Karelia), in which the amount of suitable habitat is over 40% at the landscape level. The higher diversity of polypore communities in Russian Karelia compared to adjacent eastern Finland has also been documented by Lindgren (2001), who found that species richness and abundances in most of the indicator and threatened polypore species were considerably higher in the large and pristine Vienansalo old-growth forest area in Russian Karelia than in adjacent old-growth forest fragments in north-eastern Finland.

Metapopulation models (e.g. Hanski 1999a, 1999b) may be helpful for a better understanding of the dynamics of wood-decomposing fungi, which live in patchy environments both at the stand level (in separate tree trunks) and often also at the landscape level (as the threatened polypore species occur almost exclusively in the remaining old-growth forest fragments in southern Finland; II). Metapopulation theory predicts that small and isolated habitat patches have a smaller probability of being occupied at any one time than large and well-connected patches (Hanski 1999a). In support of these predictions, the species number, the incidence of occurrence (proportion of occupied fragments) and the abundance of especially rare, threatened and near-threatened polypore species were much lower in old-growth forest fragments in Häme, with a small number of isolated old-growth fragments, than in Kuhmo, with a shorter history of intensive forestry and much higher amount of old-growth forest at the landscape level (IV). Since many of the rare and threatened polypore species were either entirely absent or very rare even in the best old-growth fragments in Häme, the results suggest that several polypore species in southern Finland are in immediate risk of going regionally extinct (Hanski 1999a, 2000). While the landscape matrix of managed forests can be used by many forest species (see e.g. Andrén et al. 1997 and Mönkkönen and Reunanen 1999), this is not the case with threatened polypore species in southern Finland (Chapter II). In the same manner, and most probably for the same reasons, a very large fraction of the endangered forest-inhabiting beetle species have already gone regionally extinct in the southernmost Finland (Hanski & Ovaskainen 2002). In polypores, which are expected to respond more slowly to environmental changes than beetles, up to 12 out of 19 critically endangered or endangered coniferous forest species (Rassi et al. 2001) are missing from the southernmost Finland (hemiboreal and most of the southern boreal zone). Of these 12 species, five have previously been recorded from the southernmost Finland and only one or two species are truly northern species, which might not occur in the southernmost Finland because of climatic reasons.

Biogeographic and climatic factors may partly explain differences in species richness and abundances of individual species between the Vodlozero, Kainuu and Häme study areas. For example, according to Kuusinen (1996) differences in climate (general humidity) has an important role in explaining differences in species composition of epiphytic lichens between middle boreal Kainuu and southern boreal Häme. In polypores the influence of climate in determining the occurrence of species is probably much smaller than in lichens, and only a few polypore species in Finland can be considered as

clearly southern or northern coniferous-heath forest species (Niemelä 2001). The vegetation zones in this study, the middle and southern boreal zones, are partly overlapping (Fig. 1) and the study areas are characterized either by indifferent (Häme) or indifferent-slightly continental (Kainuu and Vodlozero) climates, which are very similar (Ahti et al. 1968). Furthermore, the distance between Vodlozero and Kainuu and between Kainuu and Häme is no more than 300 to 500 km. On the basis of these differences between the study areas, one would not expect marked differences in species composition and abundances. Possible exceptions include five species between Vodlozero and Kainuu (*Diplomitoporus flavescens, Postia guttulata, Pycnoporellus fulgens, Rigidoporus crocatus* and *Trichaptum pargamenum*), and another five species between Kainuu and Häme (*Cystostereum murraii, Diplomitoporus crustulinus, Postia guttulata, Trichaptum laricinum* and *Trichaptum pargamenum*). Differences in the occurrence and abundances of these species between the study areas can possibly be explained by climate or biogeography. In brief, because of the very small number of such species, the differences in species richness and abundances between the study areas in III and IV can best be explained by differences in the history of forestry and in the amount of remaining old-growth forest in the respective forest landscapes.

I did not expect strong influence of isolation of the old-growth forest fragments on the occurrence of polypores in Kuhmo, because of the relatively recent fragmentation in this area and because of the expected time lag in the responses of polypores to habitat fragmentation (Tilman et al. 1994, Hanski 2000, Hanski and Ovaskainen 2002, Ovaskainen and Hanski 2002). Nonetheless, the model-derived isolation index (see Material and methods in IV for the construction of this measure) explained a significant amount of the among-fragment variation in the abundances of some of the rare and threatened species in Kuhmo (Figs. 4 and 5 in IV). Furthermore, the results in III, which show that the abundances of threatened and indicator polypore species are much lower in Kainuu than in the Vodlozero National Park in Russian Karelia, suggest that even in Kainuu, where the Kuhmo study region is located, the most sensitive species have declined although the overall numbers and abundances of threatened and near-threatened species are still much higher than in southern Finland (see also Lindgren 2001).

Even if fragmentation of spruce-dominated old-growth forests in Kuhmo is a rather recent phenomenon (Gu et al. 2002, IV), both the slash-and-burn cultivation (started in the 17th century in Kuhmo; Keränen 1984) and selective logging (started at a larger scale in the 19th century) must have degraded the quality of the forests in Kuhmo in

comparison with the natural forest landscape in the Vodlozero National Park. This difference in the history combined with the more recent old-growth forest fragmentation most likely explains the difference in the abundances of threatened and indicator polypore species between Kainuu and the Vodlozero National Park.

One of the tasks for ecologists working with habitat loss and fragmentation is to identify species and species groups that are especially sensitive to fragmentation effects (Andrén et al. 1997, Mönkkönen & Reunanen 1999, Dettki et al. 2000, Henle et al. 2004). According to Henle et al. (2004), species with several of the following traits are expected to be particularly sensitive to fragmentation: low population density, high-amplitude population fluctuations, low reproductive potential, limited storage effects, intermediate or low dispersal capacity, and specialised habitat requirements. Habitat specialists, such as polypores preferring large dead trees and/or old-growth forests, are expected to be much more sensitive to habitat fragmentation than habitat generalists (With and Crist 1995, Bender et al. 1998, Henle et al. 2004). Also the matrix of managed forests outside old-growth forest fragments is expected to be much more hostile for habitat specialist species than for generalist species (Andrén 1994, Andrén et al. 1997, Henle et al. 2004; see also II). Consistent with these ideas, rare and threatened polypore species, which prefer old-growth forests (see Fig. 2 in IV), were more sensitive to fragmentation effects than intermediate or common species, which occur also in managed forests (Table 1, Figs. 4 and 5 in IV). Furthermore, species growing on spruce were especially sensitive to fragmentation effects, and more so than species growing on pine and deciduous tree species (Figs. 3 and 5 in IV), though the data in IV are probably not sufficient to draw definite conclusions about the sensitivity of pine-associated species. Four spruce specialist species (*Amylocystis lapponica, Fomitopsis rosea, Phellinus ferrugineofuscus* and *Phlebia centrifuga*), which all grow on large fallen spruce logs and are either threatened or near-threatened species in Finland (Rassi et al. 2001), were found to be especially sensitive to fragmentation effects. These species exhibited both a significant difference in abundance between the Kuhmo and Häme study regions as well as a significant effect of fragmentation in Kuhmo (Fig. 5 in IV). Previous studies have shown that these species, especially *A. lapponica* and *F. rosea,* are also sensitive to logging (Bader et al. 1995, Sippola et al. 2001, II). *Fomitopsis rosea* and *P. centrifuga* have been shown to have reduced spore deposition and fertility of spores along a gradient of increasing impact of forestry and decreasing amount of old-growth forests from north to south in Sweden (Högberg and Stenlid 1999, Edman et al. 2004a).

The studies by Stokland (1999, 2000) on polypore and corticoid species as well as the studies by Siitonen et al. (1999), Punttila (2000) and Siitonen and Punttila (2003) on saproxylic beetles suggest that spruce specialists are more sensitive to forestry and fragmentation of old-growth forests than pine specialists. Punttila (2000) and Stokland (2000) propose that species associated with pine and spruce might have dissimilar adaptations to forest disturbance dynamics. In natural forest landscapes, stands of pine burn more often than stands of spruce (Zackrisson 1977, Engelmark 1984, Ohlson and Tryterud 2003, Pitkänen et al. 2003, Tryterud 2003, Wallenius 2004), and it may hence be that for pine-associated species, and possibly also for species using deciduous trees, the change in disturbance regime in managed forests is not as disastrous as for spruce-associated species. Nilsson and Ericson (1997) have suggested that the effects of habitat fragmentation are most severe in the case of species that occur in habitats which used to cover large continuous areas characterized by small-scale natural disturbances (boreal spruce forests; see e.g. Kuuluvainen 1994, Ohlson and Tryterud 2003, Pitkänen et al. 2003, Tryterud 2003, Wallenius 2004).

CONCLUSIONS

1) Direct short-term effect of forest fire on communities of wood-decomposing fungi is mostly destructive, and especially species growing on logs of intermediate and advanced decay stages, including several threatened polypore species, are adversely affected (I and this summary).
2) Fires can create large amounts of dead wood, which on the long-term is beneficial to a large number of red-listed species. However, the appearance of red-listed species most probably depends on the vicinity of source areas, from which the species can disperse to the disturbed areas. Since many threatened species, which have been considered to be indicator species of spruce-dominated old-growth forests, were also found in the burned areas, it may be that for some of these species abundant and continuous availability of dead wood as such is more important than the moist and stable conditions of old-growth forests.
3) Species favoured by forest fires include both ruderal species and species that thrive in dry, open forests. Some rare and threatened species are also favoured by fire (I and this summary).

4) In southern Finland the diversity of polyporous fungi is much higher in spruce-dominated old-growth forests than in mature or overmature managed forests. Threatened species are generally very rare in managed forests in southern Finland (II).

5) Diversity of different host tree types is of great importance for the presence and abundance of many polyporous fungi. Dead deciduous trees contribute greatly to this diversity (II).

6) Threatened polypore species prefer large logs of intermediate or advanced stage of decay, which are rarely found in managed forests. Cut stumps and thin logging residues, which prevail in managed forests, cannot be utilized by threatened polypore species (II).

7) In mature and overmature forests stand structure (quantity and quality of dead trees in particular) is a more important attribute for polypores than stand age. However, in overmature forests deciduous trees often become senescent and start to die, which benefits polypore species utilizing deciduous host trees (II).

8) In Häme no threatened polypore species were found from stands in which the amount of dead wood was less than 20 m^3/ha. This figure appears to represent a threshold value in southern Finland (at least in spruce-dominated, mature forests), below which the occurrence of threatened species becomes unlikely. In northern Finland, where the amount of source areas and the amount of dead wood in forests in general are higher than in the study area in Häme, this threshold value may be lower than 20 m^3/ha, whereas in large areas in the southernmost Finland the threshold value may be higher than in Häme (II).

9) The occurrence and abundance of threatened polypore species in old-growth spruce forests in Häme in southern Finland are so low in comparison with the Kuhmo region in eastern Finland that many threatened polypores have a high risk of regional extinction (II and IV).

10) In Kuhmo and Kainuu in eastern Finland, where the history of forestry is shorter and the area of old-growth forests is greater than in Häme in southern Finland, threatened polypore species have much lower abundances than in a large, natural boreal forest landscape in the Vodlozero National Park in Russian Karelia. Despite the rather recent fragmentation history of old-growth forests in Kuhmo, some threatened polypore species show a significant negative response to old-growth isolation. Hence many threatened polypore species have already suffered

in the Kuhmo area, and they may further decline in the near future because their populations may exhibit a substantial time lag in their response to loss and fragmentation of their habitat (III and IV).

11) Spruce-associated threatened polypore species are especially sensitive to the effects of old-growth fragmentation. The reason for their sensitivity may be that the disturbance dynamics created by modern forestry is most dissimilar to the natural dynamics in the case of spruce specialists, which are adapted to living in forests with infrequent fires and other large-scale disturbances (IV).

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